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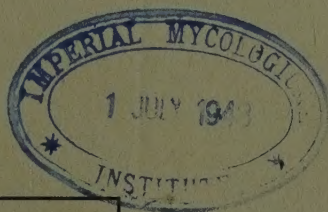
THE BOTANICAL REVIEW

Interpreting Botanical Progress

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POLARITY IN PLANTS

ROBERT BLOCH

Yale University

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INTRODUCTION

Manifestations of living matter present many problems; one of the most significant for the understanding of organic form and function is concerned with the process of orderly growth and differentiation into characteristic three-dimensional patterns. During ontogeny both unicellular and multicellular organisms develop a multitude of forms, displaying symmetries or asymmetries which differ in character. Examples of these are polarity, dorsiventrality and other axiate patterns. These terms are concerned with body forms and functions in reference to axes, centers of symmetry, *etc.*, but little is known about their protoplasmic foundation and general control.

In plants, as in animals, simple axes and axiate structures appear

very early in development. Most frequently these are "polar", since a change or gradation in character occurs along the axis from one end to the other. This condition is called "polarity", and most generally designates any internal asymmetrical state or any situation where two ends or surfaces in a living system are different.

Polarity is often visible as morphological differentiation or axiation, for example, in axes of shoots and roots ("verticibasality"—Pfeffer). Or it is invisible, physiological, and expressed in the differential behavior or reactivity of cells, tissues and organs, in the determination of the plane of cell division and cell growth, in reactions of organs to geotropic or phototropic stimuli, *etc.* If an axis of transverse polarity is added, perpendicular to the original longitudinal one, as in plagiotropic branches of woody plants, in branches of *Commelinaceae*, or in gametophytes of many liverworts and ferns, dorsiventrality results.

Polarity of shoots and roots is strikingly demonstrated in regeneration of cuttings. A stem cutting forms shoots at the apical end, roots at the basal end, and a root fragment regenerates roots at the apical regions, and shoots at its base. Statements of Theophrastus and other ancient writers (*cf.* 237, p. 199 ff.) indicate that simple experiments with plants in inverted position were undertaken long ago, and other phenomena of morphological polarity, as differential callus formation from ringing wounds of trees, were noted by Hales (76) and Duhamel du Monceau (52). However, morphological polarity was not systematically investigated until 1878 (237). Vöchting found that in isolated or inverted parts of plants environmental factors affected but little the polarity pattern transmitted from the mother plant, and a theory was put forward of innate and irreversible morphogenetic factors and forces within the plant.

The term "polarity" in relation to regeneration phenomena in animals was introduced in 1864 by Allman (4), and subsequently the term was extensively employed in this sense in animal embryology and plant morphogenesis. Vöchting held the opinion that the phenomena of polarity in plants are a result of the polarities of the individual cells composing them. Modern attempts of further-going factorial analysis have created a multitude of uses and applications of this term to widely different phenomena and processes. There is little indication at the present time as to what kind of units

are ultimately concerned with organic polarity, and in which way these may be modified, although considerable progress is constantly being made in the direction of a chemical and electrophysiological analysis of tropism and growth. At present, however, it appears impracticable or impossible to attempt to reduce the concept of morphological polarity to simple physical and chemical terms. The purpose of this article is rather to provide the student with a review of the main facts concerning the phenomena and experimental modifications of polarity in organs, tissues and cells. From these the conclusion may be drawn that foundation has been laid in many fields, although a systematic analysis and correlation of the facts has hardly been attempted.

Problems which arise in the course of this discussion are:

1. Is polarity fixed and inherited (Vöchting), or directed and more or less stably induced by intercellular correlations (Pfeffer), or induced by external stimuli and gradually fixed (Sachs), or entirely changeable (Klebs)?

2. Are the manifestations of polarity in unicellular and multicellular forms controlled by the same factors? Does polarity at one time or another during ontogeny of the organism disappear or become less stable, and may new polarities be established, for example, during sporogenesis or in meristems?

3. Does cell polarity become structurally fixed during differentiation and how does such fixation manifest itself? What are the relations of cell totipotency to organ polarity?

4. Do any of the factors known to be instrumental in growth, such as flow of nutrients or growth substances, suffice to account for axiation and polarity?

5. What are the "units" in which polarity is operating? Are they molecular, nuclear, cytoplasmic, cellular, intercellular or supercellular?

For general early discussions of polarity in plants reference may be made to several publications (237-245, 199, 96, 100, 106-108, 170, 68, 70, 128). There are also more recent discussions (278, 181, 113); in relation to growth substances (254), to bioelectric potentials (226, 48). Polarity in animals and plants has also been extensively discussed (30), and for animals alone (249, 1, 83-85, 157); also cell polarity (275, 227). Polarity in animals is also discussed in the well-known works of Driesch, Roux, and Morgan, which cannot be listed here in detail.

Polarity is expressed not only in physiological and morphological gradients of various kinds of mature axiate organs, and in the relation of the various organ polarities to each other, but also in axiate development of spores, embryos, *etc.*, in relation to pre-existing polarities in the mother organs or tissues. Therefore, a complete picture can be gained only by an extensive comparative and developmental study of the normal morphological cycle, as visualized by Goebel (69, 70). This includes both early polar differentiation and the manifold morphological differences and changes of form along the shoot axis. This is beyond the scope of a brief review which must limit itself to the more well known and significant reports on forms and stages which have lent themselves readily to experimental attack.

Whether truly apolar organisms exist, is not known. Certain amoeboid cells, for example, have no visible morphological polarity. Spherical forms, such as *Micrococcus* and *Pleurococcus*, seem to exhibit polarity in certain phases of their developmental cycle (278), not visible during the spherical stage. Some diatoms appear clearly polar, others not; filamentous forms, such as *Spirogyra* and *Oscillatoria*, possess a main axis of symmetry, and the ends appear equal. Such forms have been called equipolar. Polarity is difficult to study in many small or inaccessible cells, and conditions are not known in plants quite comparable to the situation in the animal egg where structural polarity gradually may become apparent as orderly distribution, differentiation or "anisotropy" of cellular constituents bearing a relation to an axis (*cf.* 249, 275). However, plant material offers the advantage of cells separated by rigid cellulose walls, allowing investigation of types of behavior of the individual units. In the mature, structurally highly specialized plant body, a very complex pattern is found, and distinctions have been made between longitudinal, radial and tangential polarity of cells and tissues. Certain layers of cells retain a more plastic condition as regards polarity changes, as seen in cork formation, formation of adventitious organs, and in responses obtained by well known experimental methods, such as wounding, transplantation and isolation. In the following sections reports will be reviewed concerned with polarity phenomena in normal growth and during regeneration in different plant types; various methods of experimental analysis will be also discussed.

POLARITY IN GROWTH AND REGENERATION

Slime molds. Interesting work has been done (186, 187) in the Acrasieae, e.g., *Dictyostelium discoideum*. Here the individual myxamoebae show no morphological polarity whatever, but the migrating pseudoplasmodium, consisting of many individual amoebae, has a definite and constant organization, with the terminal part serving as a sensory and directive center. The complex plasmodial structure is polarized, as is shown by the differentiation and movement of myxamoebae to specific positions, and by the fact that a new tip grafted on a decapitated plasmodium will fuse, but will not do so if grafted to the basal end, or if its orientation is reversed.

Terby (225) reported that in *Plasmiodophora Brassicae* the axes of nuclear division figures lie parallel in the somatic plasmodium. This uniform, polarized orientation is still maintained in the first sporogenic division, but disappears entirely at the second division. The evidence indicates that orientation of the nuclei is affected by a directing factor *via* the cytoplasm of the plasmodium, which is gradually lost during sporogenesis.

Fungi. In non-motile spores of fungi not many examples of polarity are known; the cells of teleutospores in rusts have germ-pores at one end.

Some transplantation experiments deal with polarity. Freeman (60) reported apolar fusion of stroma parts of *Xylaria hypoxylon*, especially when contact was made between intact tips. Successful grafting experiments were carried out by Weir (248) in *Coprinus* and in Polyporaceae; a certain polarity was seen insofar as in forms with or without stalks the side away from the substrate regenerated more readily. In *Fomes pinicola* (129) a segment from a pileus can be readily grafted back in inverted position on the parent pileus. Coalescence was complete after one month. Coalescence of an inverted segment grafted on a pileus of *Ganoderma lucidium* was also seen.

In cell threads of *Basidiobolus ranarum* polarity is extremely unstable. The terminal "step-growth" of hyphae of this fungus is normally associated with a rhythmic contraction of the protoplast in the terminal portion of the hyphae (9). Raciborski (183) showed that chemotropical stimuli, such as unilateral addition of nutrients,

will induce the basal parts of old cells to grow out and form prolongation toward the nutrient. The primary mechanism is a movement of cytoplasm in toward the stimulus; cytoplasm thus exhibits physiological polarity, followed by morphological polarity of the cell (compare the behavior of *Bryopsis*, *Caulerpa* and *Cladophora* in the section on Algae).

Algae. Visible, polar, axiate structures are illustrated by many types of swarm spores, often with a definite relation to the thallus. In *Oedogonium* the morphological axis of the zoospore is at right angles to the direction of the axis of the thallus cell in which it develops (182, 70).

In the spores of Florideae polarity is not externally manifest; it becomes visible during germination and is apparently induced by some external differential, which has not yet been determined (117, 70).

Outstanding objects for the study of polarity in algae are the fertilized eggs (zygotes) of various Fucaceae (194, 195, 266). The first indication of development is formation of a protuberance from the surface of the egg, which originally showed no indication of polarity. This is followed by cell division in a plane perpendicular to the axis of this outgrowth, which is to become the first rhizoid. In darkness only the inherent polarity of the egg is displayed; the differentiating rhizoid and axiate thallus develop in any direction with no apparent relation to external factors. In unilateral illumination by white light, however, the rhizoids generally form on the side away from the light and the first cross wall is laid down perpendicular to the direction of the incident light. Winkler (276) extended these results to *Cystosira barbata*, and determined the period necessary for induction, or rather direction, of polarity. Kniep (110) made a detailed investigation on *Fucus*.

Knapp (109) found that in darkness rhizoids were formed at that point of the egg of *Cystosira barbata* where the spermatozoid had entered.

Another phenomenon, already noted by Rosenvinge, is the so-called "group-effect": in eggs of *Fucus* which lie near each other in groups, rhizoids develop on the halves of the eggs toward a neighbor (see also 116, 91, 92, 110). In these investigations it was shown that the critical period in which polarity can be directed is early. In *Cystosira barbata* it is four hours after fertilization, and it is

irrelevant whether illumination is continued during the 12 hours which follow until germination begins (see also 109). In *Fucus* the critical period is during the 12th and 13th hour after fertilization; later the polarity is already determined, and germination begins during the 17th hour. Nienburg (163, 164) showed that the decisive factor is not direction of the light rays, but the intensity gradient. According to Hurd (91, 92), the effect is caused by wave-lengths of 4000–5600 Å, i.e., mainly the blue, and there was some evidence that ultra-violet light had the same effect. Mosebach (155) studied the effect of unilateral illumination on *Cystosira barbata*, applied immediately after fertilization; the effect begins in the blue-green, between 4900 and 5200 Å, reaching into the ultra-violet. Whitaker and Lowrance (270) reported that in populations of *Fucus furcatus* reared in the dark, at $14.75 \pm 0.25^\circ \text{C.}$, after one hour exposure to directed white light (1500 ergs/sec./cm.²), 97% of the rhizoids developed on the sides of the eggs away from light if the hour of exposure was at the stage of maximum susceptibility about eight hours after fertilization; the susceptibility period covered the time from about 4–17 hours after fertilization. Strong dosages of ultra-violet light (20,000–50,000 ergs per mm.²), predominantly of the wave-length 2537 Å (268, 269), retard or inhibit rhizoid formation in eggs of *Fucus* irradiated about eight hours after fertilization. Subsequent irradiation with white light, however, causes considerable recovery; the “protective” effect is even greater when strong white light shines on the eggs during irradiation with ultra-violet light. With moderate doses of ultra-violet light of 2537 Å, rhizoids form on the non-irradiated sides (cf. also 267). The effect is proportional to the logarithm of the dosage. However, they form at the irradiated surfaces, if exposure to white light follows ultra-violet. This indicates that ultra-violet treatment does not irreversibly incapacitate the half upon which it falls from becoming the rhizoid pole. Growth substance treatment did not restore the capability of rhizoid formation. The eggs also show a polarized response to plasmolysis (189), shrinkage occurring at the non-irradiated halves.

Formation of rhizoids at localized parts of *Fucus* eggs is promoted also by application of H-ions (257). The same author analyzed the group effect in *Fucus vesiculosus*, *F. evanescens* and in *Ascophyllum* (256). It was noted that unfertilized resting eggs of *F. vesiculosus*

can direct the plane of division in the developing eggs of *F. evanescens*. In small groups of eggs, up to ten, often the group effect was not apparent. Acidity, however, intensifies the group effect. Lowering the pH of sea water to pH 6 makes even two adjacent eggs form rhizoids toward each other; the group effect appears thus to be the result of increased ion concentration due to CO₂-production (260). The polarity also becomes directed in eggs developing in a gradient of their own diffusion products (271); in a gradient of pH the rhizoid forms on the more acid side of the egg unless this becomes too acid; in this case it develops on the less acid side of the egg (262). In agreement with these results it was found that in a medium of pH below 7.6, the group effect is positive between eggs within 0.3–0.4 egg diameters of each other, but negative in more alkaline sea water (the rhizoid forming on the side away from the neighbor) at pH above 7.6, most markedly at pH 8.4 (272). In an analogous manner does the pH of the surrounding medium control the position of rhizoids in eggs of *Fucus furcatus* of elongate shape which was obtained by gently sucking the zygotes into a small pipette while the cell wall was hardening, and then blowing them into sea water (261, 265). At pH 7.8–8.2 the rhizoids then form at or near one end of the long axis, the exactness of localization increasing with greater elongation of the egg. At pH 6.0, on the other hand, there is a strong tendency to form rhizoids toward the bottom of the culture dish (which blocks diffusion to form a gradient of products from the egg); this overcomes the effect of shape, and the rhizoids are formed near the lower end of the vertical short axis.

Temperature is also effective, since it changes the acidity due to greater accumulation of CO₂ (130, 131). Thus in a temperature gradient of 0.6–0.8° C. pro 75 μ applied to 82 eggs of *Fucus furcatus* 2–24 hours after fertilization at 14.0–15.9° C. at the egg center, 100% of the eggs formed rhizoids at the warmer sides.

Reports on the effects of centrifuging have been somewhat contradictory. In *Cystosira barbata*, both before or after fertilization, centrifuging induces the rhizoids to develop centrifugally (109). In *Fucus furcatus* (258, 259) 93–99% of the fertilized eggs, which remained stratified after 15–20 minutes of centrifuging at 3000 \times g., formed the rhizoids at the centrifugal pole. Beams (7), on the other hand, ultracentrifuged eggs of *Fucus serratus* 10,000–200,000

$\times g.$ and found no relation of the first cleavage plane to stratification of the visible inclusions. Whitaker (263, 264), however, was able to show that the stratification response of ultracentrifuged eggs is reversed with changes in external pH. At $15^{\circ} C.$ and pH 7.9–8.1 rhizoid formation is centrifugal; at pH 5.8–6.1, however, it is centripetal in 90% of the cases and at pH 6.3 the orientation is at random. The group effect may also be superposed on the stratification effect. In eggs of the related form, *Pelvetia* (132), centrifuging at 3,000, 75,000 or 150,000 $\times g.$ caused rhizoids to form at the centrifugal halves, as in *Fucus* and *Cystosira*. Most of the centrifuged eggs remained stratified and were reared in normal sea water (pH 7.8–8.2). Du Buy and Olson (49) reported that growth substance is present in high concentration in the egg and sperm of *Fucus*. In *Fucus vesiculosus* (168) the rhizoid formed toward a capillary containing growth substance; the authors suggest that growth substance plays an important role in the various responses of *Fucus* (cf. 266). Lund (133) found that the polarity of the egg of *Fucus inflatus* can be directed also by an electric field, the rhizoid being formed toward the anode; he holds that an electro-chemical polarity is the basis for the development of morphological polarity.

These investigations indicate that in the *Fucus* egg the developmental axis can be directed by a wide variety of external factors, such as gradients of light, electrical potential, temperature, auxin, centrifugal force, etc. Whitaker has emphasized that some of these factors have in common the action of a pH-CO₂ gradient, which also provides an adequate explanation for the group effect. These results support the ideas of Child (cf. 30) who has emphasized that the axiate development of the *Fucus* egg is associated with formation of a metabolic gradient with high end at the tip of the protuberance, and that this polar pattern can be readily redirected by various external differentials.

Numerous reports have dealt with polarity in algal thalli. In Fucaceae the polarity once induced could not be reversed. In other algae, for instance among members of the Florideae and Siphonocladales, numerous examples indicate that the polarity is not very firmly fixed. Thus the large cells of *Griffithsia Bornetiana*, when isolated, form shoots at the upper, rhizoids at the lower pole (231); obliteration of the direction of the polarity gradient may, however, occur after one or two days confinement in a small volume of water

(29). Centrifuging with a force of about $150 \times g$. for 24 hours induced in this plant formation of branches at the centrifugal pole, irrespective of the original polarity (203). In an electrical field rhizoid development is toward the anode (202). Polar formation of new shoots and roots occurs from cut pieces of *Polysiphonia*; *Ceramium* and *Padina pavonia* behave similarly (232). Berthold (13) demonstrated that the polar differences between apex and base are influenced by intensity of light in many marine algae. In inverted plants of *Dasycladus clavaeformis* (281), the root pole may become a shoot if exposed to stronger light intensity than the shoot pole. Transformation of shoot apices into rhizoids in weak light was noted (282) in *Sphacelaria fusca*. In *Bryopsis* the morphological expression of polarity can be changed even in old plants. In weak light the apices of unicellular and multinucleate, pinnate, branched shoots develop rhizoids (13); subsequent studies confirmed that the leaves of this plant can generally be converted into rhizoids by darkening, whatever the orientation of the plant may be. Thus Noll (166) reported that in inverted plants of *Bryopsis muscosa* complete reversal of morphological rhizoid and leaf polarity occurred, and agreed in a later paper (167) with Winkler's conclusion (277) that not gravity but light is the decisive factor. *Bryopsis disticha* is especially suitable for such tests (222); staining experiments indicated that in inverted plants there is a migration of originally apical cytoplasm into the illuminated new tip ("apiciplasm"), while "basiplasm" wanders into the new base. The author contends that in *Bryopsis* the "reversal" of polarity must be interpreted as an external morphological one only, since the actual internal, physiological polarity, expressed by the behavior of the cytoplasmic units, is retained. The reversal phenomena would not occur if separating membranes were present, as in willow shoot.

Plasmolyzing demonstrated cellular polarity in the thallus threads of marine *Cladophora* (150). The experiments indicate that each cell, which began to grow independently into a new plant after temporary plasmolysis in 20% salt solution, exhibited the original polarity of the algal thread, thus becoming an organism with rhizoid formation at its base, followed much later by swelling of the apical pole and branch formation. Borowikow (20) reported reversal of polarity by centrifuging algal threads of *Cladophora glomerata* (fresh-water); this was confirmed (38) in isolated cells

of the same plant; the inherent polarity of these cells was also demonstrated by plasmolysis experiments and regenerative behavior.

Isolated shoots or "leaves" of *Caulerpa*, a single multinucleate cell showing differentiation into "rhizomes", "rhizoids" and "leaves" have an inherent polarity pattern of a rather complicated and fixed character. The reactions have been studied in regeneration experiments (246, 95, 96, 97, 148, 45, 47, 285, 206a). Wakker reported that regenerated leaves and rhizoids formed at the base of the old leaf. Janse (96) showed that a leaf divided into three portions or wounded by transverse cuts, forms rhizoids mainly in the upper third, leaves and rhizoids from the middle and lower portions. Thus a young inverted leaf with its tip buried, regenerating leaves at its original morphological base and rhizoids in the apical regions, gives the misleading impression that polarity is here reversed. Janse contended that the thallus of *Caulerpa*, like the leaves of higher plants, is "unipolar"; a strong polar plasma stream is driven toward the base by some hypothetical "basipetal impulsion"; in inverted leaves an opposite stream due to gravity accounts for formation of new rhizomes and rhizoids (cf. 47a).

These concepts must probably be considerably modified, since conditions appear more complicated, according to investigations by Dostál and Zimmermann. The rhizomes themselves show a distinct regenerative polarity (45), new rhizoids being formed apically, new leaves in a less polar fashion. Distribution of regenerates is more polar in young leaves than in older ones (47) where proliferations may occur over the entire surface. The center portion of the leaf appears less stably polarized than the margin, since regeneration in an oval area isolated in the center by squeezing (45, 47) appears to be more susceptible to the influence of external conditions such as gravity. The cell of *Caulerpa* shows three kinds of geotropism: negative in the leaves, positive in the rhizoids, plagiogeotropic in the rhizome. Zimmermann (285) investigated the influence of gravity on horizontal and vertical polarity in the normally plagiotropic rhizomes of *Caulerpa prolifera*. Gravity induces or influences here the vertical axis of polarity, i.e., it determines the morphological dorsiventrality, expressed in the appearance of leaves on the dorsal and of rhizoids on the ventral side. The influence of gravity on the horizontal polarity axis is uncertain. The negatively geotropic leaves, however, possess an inherent vertical polarity axis which can be

modified by gravity. In all polar regenerating organs of plants the author distinguishes two manifestations of polarity: "differential polarity" and "integral polarity". The former characterizes the topographic distribution of regenerates in each fragment of an organ; for example, in fragments of willow shoots or other axial organs of phanerogams, distribution of bud and root regenerates is bipolar, or in the present case in each portion of a cut leaf of *Caulerpa* rhizoids are formed below the new leaves. The latter refers to the regenerative behavior of the entire organ. (cp. also 286). This may not be uniform; in *Caulerpa* the part of the leaf which has been used in the experiment determines the result. According to Zimmermann, the giant cell of *Caulerpa* shows the same differential polarity as a higher organized form, and, since the rhizoids in each fragment are generally formed below the new leaves, it is bipolar, not unipolar, as Janse thought.

Much speculation has resulted from experiments with *Acetabularia mediterranea* and *A. Wettsteinii* (77-82). The thallus of this plant, described as uninucleate in the vegetative state, shows considerable differentiation, consisting of a basal rhizoidal portion with the nucleus, a stalk with sterile whorls or hairs, and an umbrella-shaped apical part. Pieces from different body levels, apparently even anucleate pieces of the stalk, show remarkable regenerative capacities, and the original polarity pattern is generally maintained. Regeneration resembles that of certain hydroids, but has also analogies to organs of higher plants when short pieces of the stalk develop bipolar, heteromorphic regenerates. The author assumes the existence, between the apical and basal poles, of two opposed gradients of different specifically formative, gene-produced substances. That the effect of the hypothetical formative stuffs is proportional to their concentration is inferred from quantitative measurements of regeneration in pieces from various body levels and of varying length, with or without nucleus (82). That the nuclear products are specific is concluded from formative effects obtained by grafting a piece of stalk of *Acetabularia mediterranea* on a rhizoid containing the nucleus of *Acetabularia Wettsteinii* (81). Development of the scion then assumes the character of the stalk. According to the author, the polarity and formative effects are not due to an intimate structure of the cytoplasm nor

to a metabolic gradient in the sense of Child. The mechanism which controls the flow of the substances and their formative effects in the cytoplasm remains unexplained.

In *Sphacelaria fusca* (282) the cytoplasmic alveolar system radiating out from the nucleus is indicative of morphological polarity of the cell. This does not determine the direction of growth (physiological polarity) of the cell, however, during restitution.

Very conspicuous polarities are exhibited by cells and cell colonies of Protococcales (283, 284). Here morphological and physiological polarity generally coincide, probably due to the well differentiated internal plasmatic strand (rhizoplast); in some higher algae, on the other hand, the cell constituents are more readily shifted, and this plasticity may account for their greater variability.

Bryophytes. Little experimental evidence is available as regards polarity in spores of bryophytes. Polarity seems to be determined sometimes by the polarity of the spore itself in relation to its position in the quartet, sometimes to be induced by external differentials during germination (70, 210, 279, 280). In the spores of *Radula complanata* (liverwort), the first division wall assumes a position parallel to the incidence of light (brief statement by Geitler, 64).

In the Hepaticae, light, gravity and other environmental conditions (moisture, substrate) influence growth and form of the gametophyte considerably, as shown by recent comprehensive studies by Fitting (56-59). Induction of dorsiventrality and differentiation in germinating gemmae of *Marchantia polymorpha* and *Lunularia cruciata* are determined not only by light, but also by gravity, and (much more weakly) by the substrate and temperature. Proper combination of all three factors produces isolateral thalli. The gemmae are very sensitive toward the stimulus of gravity or light before germination, probably already while still within the gemma cup, but dorsiventrality induced at this stage is still unstable and reversible.

Gradual determination of orientation of internal polarity in the thallus is also expressed by rhizoid formation from gemmae of *Marchantia* and *Lunularia*. There are several reports concerning the effect of external factors such as light, gravity, chemical stimuli, etc. (74). In the young still bilateral thallus, the rhizoid mother

cells occur anywhere, and at first it is possible to induce rhizoid formation on either side by turning the gemmae; later this is not possible. Apparently determination of these rhizoid initials is much less fixed than that of certain trichoblasts in roots of seed plants (215). Here, according to unpublished observations by the reviewer, even high speed ultracentrifuging had no effect on root hair formation. On the other hand, in very young leaves of *Iris japonica* differentiation of stoma cells can be influenced by gravity (247).

Thompson (228) reported that in *Riella affinis* a change in orientation of the very young sporeling thallus in relation to incidence of light changes the orientation of the spindle of the first vertical division of the germ tube.

Regeneration. Vöchting (240) and his student Kreh (112) studied regenerative behavior in various parts of the Hepaticae. Thallus cells of *Marchantia* are totipotent to a high degree. Polarity is not as strongly expressed as in higher plants, and there is considerable diversity in the location of the regenerates in the different species. Organs and cells from organs with unlimited growth regenerated apically, those with limited growth basally. The Ricciaceae, for example, are strongly polar with apical regeneration from thallus pieces.

In leaves, polar regeneration is very variable. In some types regeneration is strongly polar; in others, shoots are formed over the entire surface. Polar basal regeneration takes place in perianths, except in *Aplozia*, and archegonia show a similar tendency.

Bergdolt (12) investigated the effect of external conditions on polar regeneration; gravity and light had little, centrifugal force the greatest influence. An effect on plastic materials conducted in the midrib (e.g., of *Sauteria alpina*) is suggested. Dickson (42) cut gemmae of *Marchantia* in various ways and found that the younger cells of the thallus always "dominate" the older ones as far as production of adventitious buds is concerned.

In Musci, according to Westerdijk (255a), cuttings grown under different conditions exhibit only weak polarity. Cuttings formed rhizoids at the lower pole and protonema at the upper pole, but the location of these regenerates could be readily reversed in cuttings grown in inverted position. There remained, however, generally

the tendency of regenerates to become more vigorous at the morphologically basal pole.

Pteridophytes. In pteridophytes the influence of light on development of the prothallium begins very early during germination, and there is a conspicuous and close relationship between the polarity of a single cell and the dorsiventrality of a simple organ.

Light was shown to be the directing factor in the division of the externally apolar spores of *Equisetum* (221). The first wall of the germinating spore is laid down perpendicular to the gradient of light absorption. The axis of the division figure and the daughter nuclei become arranged in such a way that the more strongly illuminated daughter cell becomes the primary prothallial cell, the more weakly illuminated one the rhizoid cell. Nienburg (165) discovered that the alignment of the nuclear spindle parallel to the direction of light takes place only after a certain redistribution of cytoplasmic material has occurred, such as the aggregation of chloroplasts at the illuminated side. Buchtien (23) confirmed the effect for bright light; found, however, that weak light operates differently. The situation here is thus very different from that in higher plants where polarity is determined very early in the microspores and has a constant relation to the meiotic divisions of the pollen mother cells.

Direction of polarity by external factors, as in *Equisetum*, has not been seen in the morphologically polar spores of ferns, perhaps with the exception of the Osmundaceae (70). Later, growth of the prothallia is largely determined by light (122, 124). Gravity was found to have little influence, with the exception of *Ceratopteris thalictroides* in which the apical cell is oriented under the influence of gravity, so that alternate segments are laid down upward and downward for some time; thus the prothallial surface stands vertically at first but soon assumes a position at right angles to the incident rays. Further development of bilaterality or dorsiventrality of fern prothallia was shown to be determined by direction of light of medium or high intensity (124, 175, 71). Rhizoids and archegonia are mostly formed on the shaded side of the prothallium. That this condition can be reversed was shown by Leitgeb and others. In very weak light isolateral prothallia may be formed; in *Polypodium vulgare* archegonia may thus be formed on both sides (175).

Bussmann (25) has shown that in clear daylight in the prothallia of the Polypodiaceae and of the Parkeriaceae (*Ceratopteris*) orientation of the 2-sided wedge-shaped apical cell and the planes of its divisions are determined solely by gravity. In the former the cutting face of the cell is parallel, in the latter at right angles, to the direction of gravity. If the daylight is deficient the direction of light influences the orientation in such a manner that in the Polypodiaceae the cutting face of the apical cell tends to be parallel, *i.e.*, the axis of the nuclear spindle at right angles to its direction, in *Ceratopteris* the cutting face of the cell is at right angles, the spindle axis parallel. In the Osmundaceae full daylight influences the orientation of the apical cell in the same sense as weak daylight directs the position in the Polypodiaceae, and here the substrate also exercises an influence insofar as the flank of the apical cell tends to be vertical to the substrate. Bussmann found that dorsiventrality in these fern prothallia is determined by light, gravity and the substrate. Compared with gemmae of liverworts, however, the influence of light is much more predominating; the effect of the substrate is weaker and that of gravity insignificant. The same factors induced dorsiventrality in prothallia of an apogamous race of *Dryopteris Filix mas* (26).

Orientation of the organs in the embryo of the Filicales is determined by its position in the archegonium and apparently is not changed by either gravity or light. In *Marsilea* (123) the direction of gravity has some influence on the position of the primary division of the fertilized egg cell. The plane of the new wall, however, always includes the axis of the archegonium around which it can rotate so as to be placed more or less at right angles to the direction of gravity. Similarly in *Isoetes* (119) gravity may, during a brief period after fertilization, affect to some extent the position of the primary wall of the embryo within the female gametophyte; the wall is here laid down somewhat obliquely to the archegonial axis, at right angles to a vertical plane including the axis.

Polarity of adventitious outgrowths on fern prothallia, under a variety of conditions, was recently discussed (2, 3) in relation to apical dominance. A correlation between gradients of osmotic concentration and the regenerative pattern was also shown to exist in these prothallia (72a).

Beyerle (14) distinguished four types of regeneration in isolated primary leaves: *a*) shoot buds; *b*) shoot buds, transitory formations and prothallia; *c*) transitory formations and prothallia; *d*) prothallia. In some leaves the regenerates occurred irregularly over the entire leaf, in others more at the leaf basis or margin, in others near the ends of the veins at the apical margin. In some ferns, however, in which at the same time shoot buds and prothallia were formed, the buds were produced mainly from the basal, the prothallia from the apical half of the leaves (*e.g.*, *Davallia canariensis* and *Nephrolepis biserata*).

A spontaneous change of polarity of the apical cell or region is indicated by several reports in the older literature, referring to natural transformations of root tips into buds. In some cases the buds apparently are formed merely close to the extremity of the root (*cf.* 142); in *Diplazium esculentum* and in various *Platyserium* species, however (196), the quadriseriate, tetrahedral apical cell of the root becomes the apical cell of the new shoot by ceasing to cut off segments on the side of the root cap, thus becoming triseriate like the apical cell of the shoot. Reinvestigation of these and analogous reports in higher plants are desirable.

Phanerogams. *a*) *Microspores and macrospores.* The polarity of microspores of both angiosperms and gymnosperms has a definite relation to the meiotic divisions and to their position within the tetrad (pollen mother cell). Details have been discussed (69, 70) and corrected (64). Various types, specific and genetically fixed, occur, the generative (prothallial) cell being formed at the side of the microspore toward the inside or outside of the tetrad (*cf.* 281a). The position of the spindle axis and thus the plane of cell division is constant for each species; it has no simple relation to the form and structure of the membrane, nor is it determined by vacuoles. It appears to be partly correlated to a polar differentiation in the living cytoplasm. In *Tradescantia*, as an effect of temperature, the division of the microspore may not be in the normal axis (200). The angle of deviation is correlated with differentiation of the daughter nuclei. In *Periploca sepium* (201), pressure on the developing mother cell determines its degree of elongation and thus the positions of the nuclei in relation to the cytoplasmic mass, and the axes of the nuclear divisions are not in constant polar relation to the axes of the meiotic divisions.

Polarity during macrospore and embryonic development is also determined at an early stage. Thus in the relation of the angiosperm macrospore to that of the macrosporangium, the egg cell pole of the macrospore and the root end of the embryo are always toward the micropylar end, and the antipodal pole of the macrospore and the shoot end of the embryo away from it. Embryo sac polarity is seen after formation of megaspores (143a). Joshi (102) reported a case of reversed polarity in the fully developed 8-nucleate embryo sac of *Woodfordia floribunda*, in a tree which flowered in October instead of in the first month of the year; the synergids at the side of the egg cell were situated at the chalazal end, the three antipodals at the micropylar pole. In the gametophyte of both angiosperms and gymnosperms, polarity appears to have a definite and continuous relation to that of the polarity of the ovule. That the polarity of the egg cell is not entirely essential as a basis for embryonic development is vividly illustrated by the not infrequent cases of polyembryony, adventitious embryony and bud formation from isolated pieces from various parts of plants. Here cells of physiological correlations widely different from the egg cell and of different organization all give rise to the same embryonic forms. This fact would seem to indicate that the same basis of polar pattern and organization is to be found in any cell and may be brought into action under conditions favorable for dedifferentiation and regeneration.

b) *Shoots and roots.* Interpretation of polarity phenomena in shoots and roots has been the object of considerable difference of opinion between early workers, *viz.*, Vöchting, Sachs, Klebs and Pfeffer. Vöchting (237) had shown originally that a stem or cutting is polarized, and he attributed this property to polarity of individual cellular components and ultimately to their molecular structure. Apex and base exist already in the embryo (243) and cannot be reversed later. Contradicting himself somewhat, however, he admitted a certain flexibility by introducing the concept of totipotency derived from histological restitution phenomena (237, 243, 244), which simply states that no living cell has a specific and unchangeable function, but retains all potencies; its function (and structure) are determined by its position in the plant body and by external factors. This concept would necessarily lead to the inference that polarities directed or fixed by internal conditions can

often be modified. Sachs (199) maintained that polarity phenomena are induced very early in development by the flow of specific substances directed by gravity; but he contradicted this idea in the second part of his publication in assuming that this flow is due to inner causes (cf. 238, 239).

Klebs (106, 107, 108) objected to Vöchting's rigid concept of irreversible polarity. In his opinion the cells of the terminal growing point have no fixed polarity, and in older parts of the stem, promotion of lateral organs is often still possible. He believed that the behavior of older portions of the shoot is the result of internal conditions which have become different in different parts of the stem under the influence of external factors. It is thus doubtful that any inference can be drawn as to actual conditions in the growing point or ovule from the correlative polar condition of a mature stem portion in which differentiation has become somewhat fixed.

In the few investigations on direct regeneration of growing points no attention has been given to possible changes of polarity, nor has culture of excised parts of the growing point yet been carried out from this point of view. The factors which determine the definite polarities exhibited by dividing apical cells are not known. Occasional differences in the method of division or "spontaneous" alterations have been reported to occur in the same type of apical cell. Some notes in the literature seem to indicate the possibility of a spontaneous change of a root-growing point into a shoot-growing point (e.g., 65; *Neottia*, *Anthurium longifolium*). The majority of investigations have been concerned with polarity in relation to lateral organ formation, callus formation, and cell and tissue behavior during transplantation. Unfortunately, critical evaluation of many reports is not possible due to lack of anatomical data.

In order to obtain reliable results in polar regeneration experiments, material should be used in which the disposition to form roots or shoots is the same along the axis, and the conditions must be uniform. There are, however, considerable differences in the expression of polarity in stem cuttings of different species. Structural peculiarities, such as formation of roots from the nodes of monocotyledons, may obscure the polar behavior of cuttings. Especially the stage at which the cutting is taken from the mother plant may influence the distribution of adventitious structures, since in

the older parts initials already formed may cause the sharp polar contrast to become obscured (*e.g.*, 237, 151). It is necessary also to take into account differences in the polar reactivity of tissues giving origin to axillary buds, adventitious buds or roots, as well as the fact that a different complex of conditions may control each of various phases in the new formation of polar structures, such as formation of meristems, further development of primordia, and final differentiation into shoot and root structures. With favorable material the influence of external factors, such as gravity, centrifugation light, moisture, oxygen and growth substance application, may be studied.

Vöchting's fundamental regeneration experiments with willow cuttings and other woody plants showed that there is a general polarity in shoot and root reproduction, especially in young branches. If a stem is cut into smaller parts, each level may become either a morphological apex or base in the cutting, with no apparent relation to the position which it occupied before it was taken from the mother plant. But root formation is locally promoted by water contact or humidity or by darkness. Gravity also is of some influence, for in inverted cuttings the adventitious organs occupy a more extensive area than in normal position. Klebs (106) stated that in *Salix alba vitellina* root formation could be induced by water anywhere. Küster (115) confirmed the favorable influence of water and also of oxygen. Freund (61) stressed the influence of humidity in various herbaceous plants; Ursprung (235) reported influence of water and oxygen in *Impatiens Sultani* which regenerates in strongly polar fashion.

Root formation is mostly characteristically polar, but shoot formation may be much less limited to one end of the cutting or not at all, for example, in *Begonia* (44). Massart (145) investigated 30 species, 11 of which regenerated shoots and roots satisfactorily in normal, inverted and horizontal position. The following four types were distinguished: (a) Both strongly expressed shoot and root polarity present, *i.e.*, the adventitious structures occurring strictly at the respective poles (*Rosa indica*, *Salix viminalis*, *Mühlenbeckia platyclados*, *Sempervivum dendroides*); (b) No bud polarity, root polarity present (*Kleinia Autheuphorbium*); (c) Bud polarity present, no root polarity (*Rosa arvensis*, *Rubus caesius*, *Jasminum nudiflorum*, *Cereus hamatus*, *Opuntia*, several sp.); (d)

Weak bud and root polarity (*Aloë frutescens*). Bud polarity was generally less strongly limited than root polarity. Root polarity has a relation to the growth habit of the plant, some species with pendant branches readily rooting at their apical ends. However, no anatomical investigation was made.

An anatomical explanation of such variable polarity was attempted by Plett (173). He found polarity well established for shoots arising from bud initials, such as axillary buds, and for endogenously formed adventitious roots. Of 410 investigated species, 67 species produced roots only, 38 regenerated adventitious buds, and 27 also roots, but only in *Acanthus mollis* and *Salvia silvestris* were adventitious buds strongly limited to the apical end; they were formed basally in four species, and they occurred in all others rather irregularly at the apical or basal wound callus and in the cortex or even the epidermal region. These are *Rudbeckia laciniata*, *Bottionia latisquama*, *Centaurea calocephale* f. *aurea*, *C. rupestris*, *Scabiosa arvensis*, *Salvia sylvestris*, *Physostegia virginiana*, *Solanum nigrum*, *Lycopersicum esculentum*, *Nicotiana tabacum*, *Sinningia purpurea*, *Acanthus montanus*, *A. mollis*, *A. spinosus*, *A. longifolius*, *Littonia argyroneura*, *Passiflora caerulea*, *Cleome spinosa*, *Maurandia lophospermum*, *Begonia*, several species of *Peperomia*, *Torenia*, *Apocynum*, *Lysimachia*. The sprouting of axillary buds already present was always in a polar fashion. The polar formation of endogenously formed adventitious roots and the irregular distribution of adventitious buds from the callus and the more superficial cortical region seem to suggest that the inner layers of the internode are more strongly under the influence of axial polarity than the cortex and the callus masses.

Veh (236) investigated polarity in shoot pieces of *Costus speciosus*, Brieger (21) in cuttings of *Manihot*. Beattie and Thompson (8) noted proximal dominance and sprout growth in cut pieces of sweet potato.

Schwanitz (206) investigated polarity phenomena in rhizomes of *Lathyrus pratensis* and *Agropyrum repens*. Shoots and in *Agropyron* also roots regenerated from the anterior ends. Since differences in the regenerative capability of successive pieces of rhizomes depended on the time at which these were cut, the presence of some substance appears likely, which at first is distributed uniformly, but is gradually transported through the tissues toward

the anterior end. Gravity has influence on the conduction and distribution of this substance. In a similar manner in dormant horseradish roots there is, according to Lindner (127a), no polar distribution of factors that cause either root or bud initiation. Polar distribution of such factors, however, occurs after the root is placed under conditions favorable for regeneration.

Differences in the intensity of callus formation at the upper and lower margins of ringing wounds were already noted by Hales and Duhamel. In stem cuttings there are qualitative and usually also quantitative differences in the formation of the calli at the apical and basal cut ends (*e.g.*, 156, 114), the basal callus usually being more vigorous. Shippy (209) studied polar differences in callus of stem and root cuttings of apple. There are varietal differences.

Tittmann (230), however, saw no difference in the amount of callus in *Populus pyramidalis*, if kept under the same condition. Simon (212) stated that in *Populus* polar callus formation is not quite definite. The basal callus is stronger under highly humid conditions, but later often the apical callus becomes more vigorous. Under dry conditions the apical callus was stronger from the beginning. Anatomical differences occur, the "primary" growth is greater at the apex, but the second phase of meristem and root formation is greater at the base. Here also wound wood was formed, while at the apex vascular connections are established with the shoot initials.

Polar restitution phenomena also vary considerably in root cuttings. Trécul, in 1847 (233), reported that in *Maclura aurantiaca* endogenously formed buds and roots arose at the respective polar ends. In *Ailanthus glandulosus*, however, polarity was less determined. Adventitious buds occurred in three locations, endogenously and in the inner and outer part of the cortex.

In cuttings of roots of *Taraxacum*, buds are formed at the basal (proximal) pole or shoot end toward the stem, while a small amount of callus with a few roots appears at the apical (distal) pole. Wiesner (273) reported that in pieces 5–6 cm. long, shoots were formed on both cut ends, if the cuttings were kept moist and illuminated. Goebel (66, 67a, 68) obtained shoots at the apical end by enclosing the base in plaster of Paris or sealing wax. Küster (114), Timmel (229) and Czaja (39) noted that the callus appears more rapidly at the basal pole. Küster found, however, that the polar

difference in callus formation can become masked by external conditions; when the apical end is kept in air of high humidity and the basal pole in water or sand, the apical callus becomes more vigorous. Shoot formation may be influenced correspondingly. This situation is comparable to that in stem cuttings, and the natural polarity in such cases is not actually reversed. Němec (160, 161) noticed the effect characteristic for very short root pieces to form buds on both ends, in his opinion due to traumatic overstimulation. Later (162) he found that water treatment also promoted bud formation on both ends in 45.5% of the cases, and chloralhydrate had the same effect in 60% of the treated roots. Light also promoted bud formation. Czaja (40) induced bud formation at the apical end by repeated decapitation of the basal end and attributed this effect to growth substance correlations.

Schouteden-Wéry (205) investigated effects of light and gravity on bud polarity in root cuttings of *Cichorium*. The technique was to illuminate or darken either the entire cutting or its proximal or distal poles, in normal or inverted position; buds were thus produced from the proximal pole in any position. Light and gravity may counteract the innate polarity insofar, as they may promote bud formation also at the distal pole.

Magnus (143) studied polarity in callus formation of carrot roots. Root cuttings of *Crambe maritima* show excellent polarity in callus, shoot and root formation (101). Pieces 5–10 cm. long show roots formed from apical callus and shoots from basal callus; this polarity is maintained in inverted cuttings. However, when roots are split longitudinally, the influence of gravity after inversion becomes apparent in shoot production from lateral cambial calli, the green bud-forming portion of the callus now becoming more vigorous and extending much further toward the root pole than in normal position. Centrifugation toward the shoot pole is followed by bud formation as well as root formation at the root pole. As in *Taraxacum*, small sections 2 mm. long or less produced shoots on both ends. In root pieces split longitudinally, bud formation can be promoted locally by rise in temperature. The author discussed the results in relation to respiration and Child's theory of metabolic gradients.

c) *Long term inversion experiments, transplantation, wounds and histological changes.* Light, gravity, moisture, oxygen and other factors influence the area and formation of adventitious organs

and other growth activities even in highly differentiated stages, and it is to be expected that more extensive histological changes occur in plants which are grown in inverted position for considerable time. Kny (111) successfully cultivated cuttings of *Hedera Helix* and of *Ampelopsis quinquefolia* in inverted position for several years; a perfect reversal of organ formation could not be obtained: there remained a tendency of buds to develop near the soil. Strasburger (224) grew inverted cuttings of *Salix stipularis* and *S. alba* for over one year. Lundegardh (138, 139) emphasized the difficulty of changing the ontogenetically induced (structural) polarity in *Coleus*. Pont (174) reported adaptation to new conditions of *Salix babylonica*, whose shoots were dipping into water and had become rooted at the apex. In a two-year-old willow cutting (243) the inverted portion failed to grow and gradually died back, probably due to the fact that the strongest lateral shoot was just above the ground. Graham, Hawkins and Stewart (72), however, reported successful establishment of an inverted cutting of *Salix alba* which was planted in 1923, grew until the end of the experiment in May 1934, with two strong leaders at the top, the lower of which had assumed dominance in 1926.

Considerable rearrangement of tissue elements has been shown to take place in such abnormally grown plants, particularly at the attachment points of branches and roots. Vöchting (245) described such internal whorl or tumor formation in *Salix fragilis* and other species and based this phenomenon on the assumption of an innate polarity of cell elements with positive and negative growth affinities, a concept which has been criticized by various investigators. Previously Vöchting (242) had described in inversely grafted tissues of *Cydonia japonica* and *Beta vulgaris* a similar formation of irregular aggregates during reorientation of tracheal connections. These indicated the existence of a longitudinal and a radial polarity in the cells. Dostál (46) reported that the conditions in *Beta vulgaris* are even more complicated; he assumed the existence of a tangential polarity, due to local unequal growth conditions under the influence of the position of the vascular bundles. Mäule, Neeff and Rothe (198) confirmed Vöchting's findings. Mäule (146) and Neeff used Vöchting's theory of cell polarity to explain the behavior of cambium cells in wound wood, Neeff particularly for the phenomena observed after decapitation of the main stem (158), and in

decapitated roots, root grafts, *etc.* (159). Jaccard (94) contested the validity of Vöchting's explanation, and attributed the twisting effects in the cells to mechanical factors (*e.g.*, in pith of *Picea excelsa*). Twisted cells also occur in other pathological tissues, such as intumescences, galls, *etc.*, where there is no polar organization at all; it appears suggestive that in decapitation (Neeff) the change in distribution of sap flow might influence the direction of growth of the cambium cells. Timmel (229) found these whorl formations in the normal callus of roots of *Taraxacum*, where mechanical factors are hardly operative. MacDaniels and Curtis (141) mentioned changes in orientation of cambium cells in ringing wounds on apple trees. Janse (98) noted that the direction of growth of the cells changed under a strip of bark left across a ringing wound in *Acalypha*; the change was gradual and cumulative in each successive layer cut off by the cambium. Tupper-Carey (234) described the stages in the change in the direction of growth of phloem and xylem elements from the vertical to the horizontal across such tissue bridges in *Acer pseudo-platanus* and *Laburnum vulgare* and suggested the following factors responsible for the changes in the direction of growth: release from internal pressure; increased supply of oxygen, followed later by a reestablishment of the pressure and the normal oxygen supply when the surface has callused over; the movement of food downward, and renewed cambial activity in a basipetal direction.

Merjanian (147) studied polarity in grafted canes of vines. Janse (99) split shoots of *Helianthus annuus* longitudinally and regrafted the halves in more or less laterally shifted position. Thus bundles in separate halves came to lie side by side in inverted orientation. Connections were, however, made between xylem and xylem, and phloem and phloem, indicating a directing stimulus and reversible radial polarity of cambium cells. Colquhoun (37) reapplied pieces of bark and buds in inverted position in *Casuarina paludosa*. Inverted branches grew like normal ones; the anatomical investigation showed that the cambial cells joined freely and continued growth regardless of inversion, while the wood fibers and vessels turned and twisted in the same manner as described by Vöchting. They are apparently unable to unite with their opposite ends, and it appears that, in Pfeffer's sense, the polarity of cambial cells is at first unstable but is gradually impressed on the wood formed by it,

whose elements then show this effect by their tendency to keep translocation and water conduction in the same orientation as the original polarity. Such fixation, in the reviewer's opinion, might well be related to changes in properties of the cell wall, as also expressed in "Spitzenwachstum" and other forms of differential growth.

The general basipetal tendency of differentiation, characteristic for cambial activity, manifests itself also in the polar reconstitution of cut vascular bundles. Simon (213) found that the redifferentiation of tracheids in interrupted internodal vascular bundles in herbaceous Dicotyledons generally starts at the basal ends of cut bundles and proceeds toward the apical ends of the cut bundles below or toward uninjured bundles. Redifferentiation of tracheids may take place either directly or *via* division of parenchyma cells. The same behavior was found for phloem of herbaceous Dicots by Kaan-Albest (103).

d) *Leaves*. Most isolated leaf cuttings form adventitious shoots or roots or both at their bases and thus do not exhibit any distinct bipolarity. This behavior differs from that of shoots and roots, and Vöchting thought it was associated with the limited growth of leaves. Goebel (68) correlated this behavior with the direction of the food transport. However, there are obvious exceptions to this rule, *e.g.*, in *Drosera* (10), in which regeneration is apolar. Other examples were described by Hagemann (75); shoots could be obtained from the apical cut surface of inverted leaf cuttings of *Achimenes grandiflora*, sometimes also in *Begonia isoptera* and *Torenia Fournieri*. Inverted leaves of *Achimenes* with the tip left intact regenerated at the base only. It was suggested that in these cases the inducing factors were humidity and the wound stimulus. The conclusion to which the author came after investigating the regenerative behavior of isolated leaves of 1204 species was that the location of the regenerates is determined mainly by the anatomical structure. Wound stimulus and humidity may have some effect, but light, gravity, contact and accumulation of nutrient material in the leaf have no influence on the location of the adventitious structures.

Wildeman (274) reported on bud formation in various leaf blades and petioles of monocotyledons; here they appeared generally on the face of the leaf which was in contact with *Sphagnum*. Prevot (178) noted that in certain leaves of *Begonia Rex*, which had been grown

with a manure apparently containing certain growth substances, regenerates appeared irregularly at any place, without wounding or cutting the veins.

Freundlich (62) confirmed for leaves the basipetal type of restitution of cut vascular strands described for stems by Simon. Redifferentiation began at the basal ends of cut bundles, even in lateral veins of higher order.

According to Arens (4a), leaves of certain submerged water plants showing little indication of dorsiventrality and histological differentiation cause nevertheless changes in the medium different on the upper surface from that on the lower side, thus indicating physiological polarity.

e) *Cells: growth, division and cytoplasm.* Many cells, such as root hairs, certain wood fibers, callus cells and tyloses, show a local, differential or intrusive type of growth (216). This may be associated with polarizing condition in the cytoplasm or cell wall, but so far comparatively little is known in general as regards the interrelation of the fine structure of protoplasm and the changing cellulose patterns in cell walls (37a, 43a, 175a, 177). At any rate, certain relations seem to exist between polarization of the cytoplasm and orientation of the mitotic figure, on the one hand, and direction of growth of the cell, on the other hand. These are, however, not always evident.

In a number of cases in normal and pathological tissue differentiation, cells exhibit definite polarity with regard to location and orientation of the division, which is distinctly unequal. Examples are stoma divisions, root hair divisions and certain wound meristem divisions. During division of stoma mother cells in leaves of monocots the smaller cell is formed toward the growing leaf tip; the last meristematic division of superficial cells in certain grass roots (215, 216) is often markedly unequal and gives rise to a small trichoblast toward the tip of the root. It was shown (215) that the degree of polarity exhibited here is more or less constant for each species and a definitely maintained genetical feature. The mechanism of these unequal divisions is apparently correlated with the method of growth of these cells, in particular with an anisotropic distribution of cytoplasm and migration of the nucleus toward the distal end of the cell (215, 216). Miede (149), who centrifuged leaves of *Allium cepa*, found that the plane of division in stoma

mother cells could thus be changed. This could also be achieved by wounding. It is now generally known that the plane of cell division can be directed by wounding (*e.g.*, 16, 17) and a new polarity induced. The first visible change, readily observable in highly vacuolate cells, is a movement of the nucleus into the center of the cell as well as a change in distribution of the cytoplasm (217, 218). A cytoplasmic diaphragm, the phragmosome, is formed parallel to the wound surface, later the nucleus undergoes mitosis, and the spindle axis is oriented vertical to the wound surface. Polarity thus appears to be determined earlier in the cytoplasm than in the nucleus. In some cells, such as cambium, pericycle cells, and cells surrounding vascular strands, and in some other cases, polarity of the cytoplasm is not so readily directed (17). Associated with or following cell division, directed wall growth occurs, often toward the wound surface, but according to the reviewer's observations, in certain thick-walled or prosenchymatous cells the nature of the highly differentiated cell wall seems to offer resistance to a renewal or change of growth (*e.g.*, 16), while the cell content, as expressed in the redistribution of the cytoplasm and the plane of division, readily submits to it. These observations are in agreement with Pfeffer's idea of a changeable axis of polarity of the protoplasm with regard to a fixed cell membrane (170), and may possibly explain phenomena of apparently stable cell polarity exhibited in the transplantation experiments of Vöchting.

Summarizing numerous observations on polarity in growth and regeneration, it would appear that frequently in unicellular forms and in individual vegetative cells of multicellular structures polarity changes occur, and that determination or direction of the axis and morphological expression of polarity can here often be effected by external differentials. In differentiated and specialized plant forms and patterns as a whole, on the other hand, attempts to change or redirect the general organ polarity have met with little success, apart from local changes. Polarity phenomena at the supercellular level, therefore, appear as more rigid and less reversible properties, associated with the general structure.

PHYSIOLOGICAL MANIFESTATIONS OF POLARITY

Closely associated with polar differentiation and with natural and regenerative organ formation are a great number of physiological

phenomena, such as flow of solutes and assimilates, gradients in osmotic concentration and metabolism, respiration, pH, movement of auxins and distribution of other growth factors, and the generally present bioelectrical potentials. These processes or phenomena are obviously important factors in normal growth and polar regeneration. In spite of the considerable progress made in physico-chemical analysis of plant physiological correlations, no definite causal relation has been shown to exist between any of these factors and the phenomena of morphological polarity. Not all investigators seem to have sufficiently distinguished between the possibilities that any of these factors are primary polarizing ones and independent variables or that they are merely secondary expressions of more complicated integrations or some still more fundamental, but yet unrecognized polarity. No doubt these relationships will be better understood as our knowledge of the nature of both the structural and functional sides of plant pattern increases.

Nutrient movements. Some of the numerous papers on translocation of substances have been concerned with morphological polarity. For example, Goebel (66, 67, 68, 69) discussed polar regeneration in shoots, roots, leaves, rhizomes, fern prothallia, etc., and ascribed the effects mainly to conditions of nutrition. Differences in direction of flow of substances to "centers of attraction" for constructive material should explain the differences of polarity in these organs. This theory may serve to explain the maintenance of polar physiological events in a certain direction and quantitative control of organ regeneration, but obviously does not suffice to explain polarity. Simon (214) suggested that in leaves polar regeneration is correlated with basipetal movement of carbohydrates, and this may be due to polar differences in the conductive tissue (*cp.* also 11). Janse (98, 100) assumes an inner force, the "basipetal induction", which drives the flow of food in a basipetal direction. Hagemann (75) concluded that generally in leaves the induction and location of new formations are not controlled by accumulation of nutrients, but by an innate structural property. Similar views were expressed for roots (140) and for internodes (173). Silberschmidt (211) noted accumulation of proteins at the base of cuttings during callus formation. Schwanitz (206) found that differences in protein content appear gradually during polar regeneration in rhizomes of *Lathyrus* and *Agropyron*. They do

not control polarity, but are probably associated with greater metabolic activity in regenerating regions.

Instances of polar transport of fluorescein in hairs and in phloem of leaves and stems have been reported by Schumacher (205*a*) and Both (20*a*).

Basipetal cambial activity. It is known that cambial activity has a general tendency to develop in a morphologically basipetal direction, perhaps in relation to activation by auxin (*cf.* 254, 5*a*). Cambial activation, on the other hand, is not necessarily basipetal, as shown by wound healing and regeneration experiments. Cambial activity begins locally at the base of dormant cuttings (220), with no relation to the presence of buds which are generally correlated with root formation (125, 126). In ringing experiments on roots of *Populus tremuloides* (22) the direction of cambial activity was also modified under certain conditions. Priestley (179, 180) and Priestley and Swingle (181) associate polar regeneration phenomena in shoot and root cuttings with basipetal cambial activity already present in the mother organism.

Formative substances. Already suggested in animals by Bonnet (18), the existence of root and shoot forming substances in plants was assumed by Sachs (199) and more recently by Hämmerling (77–82), Went (*cf.* 254) and others, in order to explain polarity and qualitative differentiation. The driving force was considered to be gravity (199), or an innate polar factor. The existence of such substances was questioned by some (*e.g.*, 238, 239, 151–153, 181, 30). Vöchting showed that gravity is not effective, but no other mechanism has been found sufficient to explain the polar flow of the hypothetical substances. One objection has been that on some occasions such substances were supposed to explain polar regeneration phenomena, but on other occasions it was assumed that their directed flow is the result of polarity. The other objection is that so far no substance has been isolated or synthesized which has direct organ-forming effects. Similarly, the concept of growth-inhibiting substances as instruments of correlation has not been too fruitful, and Loeb (128, *cf.* also 169), who made considerable use of this idea in interpreting correlation and regeneration in *Bryophyllum*, later emphasized the importance of “initials” and thus the structural rather than the functional aspect of plant organization.

Polar transport of auxin and auxin concentration. Directed transport of auxin has been suggested by several investigators to be either an expression or a determinative factor in polarity. Polar basipetal flow of auxin under normal conditions in coleoptiles and many axiate organs has been demonstrated (cf. 219, 254, 255). Less definite are data concerning transverse movement, though considerable formative importance has been attributed to it by Borgström (19). In inverted cuttings of *Tagetes* (253) after 21 days auxin was observed to flow not only in the original basipetal but also in the new apex—base direction. Physiological transverse polarization and depolarization of cells by external stimuli was suggested long ago in tropistic growth reactions (55, 31, 32), but the exact mechanism is still unknown. These reactions involve possible lateral movements of auxin, changes in electric potentials, and perhaps differentiation phenomena, such as formation of lateral roots on the convex sides of curved roots (73). While most investigators assume that polarity of the plant is the primary factor, transport of auxin and associated growth reactions of the cells and tissue secondary, Czaja (40, 41; cf. 251) and Borgström (19) suggest that polarity is the result rather than the cause of directed flow of auxin. This assumption is based on the effect of unnaturally high concentrations laterally applied, which are associated with inhibition of normal longitudinal cell expansion and with new growth in radial direction. Changes in the cell wall under the influence of auxin have been reviewed (e.g., 43, 87).

Went (250) put forward a general physiological hypothesis of polarity, based on basipetal polar transport of auxin and the electric 2-pole character of plant axes. It is suggested that sufficiently large electrical forces are instrumental in an electrophoretic transport of anions, such as auxin toward the positive plant base, and of other positive particles toward the negative plant apex. Went found that acid dyes move more rapidly toward the base, basic ones toward the apex. Babička (6) also, for example, showed that the character of substances exosmosing from the basal and apical ends of shoots of young plants of *Lupinus albus*, *Avena sativa*, *Aesculus hippocastaneum*, and of branches of *Tradescantia zebrina* and *Salix viminalis* was in agreement with this view; the substances exuding from the apical region were more basic, those from the base more

acid. However, further investigation to be discussed in the following section did not confirm the consistent relation between electric potential differences and the flow of auxin demanded by the hypothesis; for example, in the same tissues simultaneously polar flow of auxin and non-polar flow of other ions may occur (252).

Statements as regards direction of flow of auxin in roots have been somewhat contradictory. According to Cholodny (33), growth substance can enter the elongation zone of corn roots only in a basipetal (proximal) direction. Both polar and non-polar auxin transport have been reported for leaves, the former in leaves of *Nicotiana* (5), the latter in *Coleus* (118). In *Nicotiana* auxin concentration toward the base of the leaf is correlated with the growth intensity pattern.

Another aspect of auxin in relation to polarity is that of concentration and is based on the well known observation that comparatively high concentrations of auxins externally applied favor root formation rather than shoot formation, while low concentration favors shoot formation. If the theory is correct, it is to be expected that in cuttings or parts of cuttings depleted of auxin, shoot formation occurs, and external manifestations of polarity may be influenced in this way. Many experiments with shoots and root cuttings reported in the preceding sections seem at least not to contradict this hypothesis.

Fischnich (53) showed that application of growth substance will produce roots from an apical stem callus where normally shoots are formed. Subsequently (54) he found that in inverted cuttings of *Populus nigra* var. *pyramidalis* shoots were formed at the original base and that similarly shoots occurred at the lower margin of a short apical piece above a ringing wound. Low auxin concentration, in one case due to inverted position, in the other due to the shortness of the piece, is suggested. Callus sometimes formed on isolated pieces of bark also gives rise to shoots. Howard (89, 90) suggested a similar effect of the auxin concentration in *Brassica*. According to Zimmermann and Hitchcock (287), buds are produced from isolated pieces of both bark and wood of disbudded stem cuttings of *Althea*. Rappaport (188) noted that apical root formation in *Eurya japonica* cuttings can be induced by application of growth substance to the apical end, but the effect cannot be transmitted from the treated base.

The characteristic of very short root pieces of *Taraxacum* or *Crambe* of forming shoots on both ends, the effect of basal decapitation of forming buds at the apical end discussed in the preceding section may be explained in the same manner. Repeated decapitation or X-ray treatment (172) of apex and base in cuttings of *Crambe maritima* induced shoot formation at the apical root end (171, 223). Subsequent application of indoleacetic acid induced root formation at the apex.

It should be mentioned that local promotion of adventitious roots by application of growth substances (*e.g.*, 120, 121, 127) is not a reversal of the general structural and physiological polarity of an organ any more than the local stimulation with water or other factors previously discussed. It rather involves a local stimulation of initials and local changes in the polarity of cells which are induced to divide. Such method, however, may be useful in attempts to establish cuttings or seedlings in reversed position (27, 28).

Bioelectric potentials. All cells and organisms have definite electric polarities. A discussion of the significance of electric potentials in biological processes in relation to morphological polarity and polar regeneration is bound to suffer from uncertainties which still exist as regards the nature and origin of the potential differences (P.D.) themselves. Discrepancies in results have also often been due to various methods of measurements employed. For comprehensive accounts of results in this field reference is made to reviews by Dubuisson (48) on cellular polarization and depolarization in relation to protoplasmic surface, permeability, *etc.*, by Thomas (226) on electric polarity and regeneration, to a recent paper by Blinks (15), and to tables by Bünning (23a).

According to Lund and his co-workers, bioelectric potentials in polar plant tissues are oxidation-reduction potentials developed at cell surfaces by the respiratory mechanism of the cell; the magnitude of the E.M.F. at any locus or at any instant is determined by the dynamic balance between oxidation and reduction ("flux equilibrium") (*e.g.*, 135); the theory is based on the relation between P.D. and the reduction of the P.D. by KCN, ether and chloroform. According to Osterhout, the P.D.'s are diffusion potentials; this interpretation is based on the effect of salts and certain organic substances at the inner and outer surfaces of the protoplast. Other investigations (144, 137, 192) indicate that the P.D.'s of a given

length of tissue equal the algebraic sum of the P.D.'s of each of its individual cell components. Bioelectrical currents have been suggested as possibly acting as a mechanism in cell correlation (134, 135) and in functional and morphological polarities (193).

As previously mentioned, the assumption that polar transport of auxin ions from the negative plant apex to the positive base is caused by an electrophoretic mechanism could not be experimentally confirmed (252). Clark (35) found that external application of a potential opposite to the inherent one did not affect the polar flow of auxin in the *Avena* coleoptile. Furthermore (36), sodium glycocholate entirely stopped polar auxin transport but did not affect electrical polarity, semipermeability, protoplasmic streaming or accumulation of inorganic ions. Cholodny and Sankewitsch (34) expressed the opinion that auxin is not transported as an electrolyte but that the effect of electric current is indirect through the complex system of the living protoplasm. According to Du Buy and Olson (50, 51) the effect is primarily on the protoplasmic streaming and thus on the transport of auxin.

Ramshorn (184, 185) finds a major difficulty of Went's hypothesis in the fact that plant regions of greater growth are really electropositive, and not negative, to regions of lesser growth. Shoot tip and root tip are positive, while their base is negative. If auxin is transported electrophoretically, the direction of flow should then be toward the apex and not toward the base. Electropositivity of regions of greater growth to more basal regions was also shown by other workers (134, 144, 136, 193, 226). This also applies to the *Avena*-coleoptile; in young coleoptiles the tip is positive, in older coleoptiles it is the middle region, and in coleoptiles grown in darkness, such as used by Clark, the base is positive, due to increased growth of the mesocotyl.

The bioelectrical potentials associated with normal growth undergo certain modifications during processes of wound healing and regeneration. Several studies have been made on herbaceous plants, e.g., in *Phaseolus multiflorus* (190, 191), hypocotyls of *Helianthus annuus* and *Pisum sativum* (104, 105), petioles of *Coleus* (86, 226) and stem pieces of *Bryophyllum calycinum* (226). Generally, wounding results in temporary negativation of the organ, tissue or cell (traumatic current), and in permeability changes. Thomas (226) concluded that if the hypothesis of diffusion poten-

tials is correct, variations in electrical potential differences during regeneration are caused by alteration of the properties of the membranes, and that therefore the phenomena of polar regeneration in cuttings are correlated with typical changes of the membranes at the base, preceding the activity of the meristems.

Morphological polarity has been directed by application of electrical currents in eggs of *Fucus inflatus* (133) and differentiated thallus cells of the red alga *Griffithsia Bornetiana* (202). In both cases rhizoid development was toward the anode. In *Griffithsia* a migration of chromatophores took place toward the anodal side of the cell, and the author suggested that the current acts in morphogenesis by moving particles of different charge.

A view somewhat divergent from most investigators is held by Burr who believes that electric fields control and regulate the physico-chemical process which establish morphological pattern. Thus in the frog's egg electropotential differences were demonstrated prior to the appearance of visible differentiated structures (24), but the mechanism by which the electrical field forces exert formative effects specific for the organism still appears obscure.

Axial gradients. Axial gradients of various kinds are among the earliest and most general manifestations of differentiation and are of equal prominence in the later stages of development of the organism. Their nature has been discussed extensively, especially for animals, by Child (30). Some of these have been mentioned in the preceding chapters.

Direct influence on differentiation has been suggested by Rothe (197) who reported that in the stem of *Symphoricarpus* the early formed leaves become stunted, owing to greater osmotic pressure of the growing tip, which brings the apex into competition for the limited water supply. In corn stalks (93) concentration of solutes is least in the basal internodes and increases upward, which is in agreement with analyses reported by other investigators for trees.

The $\frac{C}{N}$ ratio gradient present in the axes of plants is responsible for polarity phenomena, according to Hicks (88). N tends to travel upward, C downward, even in inverted shoots; but this relation may indicate only a parallelism, not a causal connection.

Child has long emphasized the general rôle of metabolic gradients. He has pointed out how regional differences and tissue changes,

polarities and symmetries, may arise and may often persist on the basis of early established physiological, metabolic, axial gradients initiated by differentials and factors in the environment (30). From the fact that polarities can often be obliterated and redirected by external differentials, he infers that inherent properties of protoplasm alone, molecular, colloidal or otherwise, do not constitute a basis sufficient to explain developmental pattern on an anatomical level. The characteristic configurations of the patterns established, however, are determined by the specific constitution and the condition of the individual protoplasm.

PROTOPLASMIC FACTORS

It may seem fitting toward the end of this article to raise anew the question as to what the decisive factors are, which in this protoplasmic organization under the influence of external forces direct its differentiation and mould it into definite patterns. Answers and suggestions have been manifold, reflecting the considerable progress made in physiological and cytological analysis of cellular activity since Vöchting; none of them has given a satisfactory answer, emphasizing the rudimentary state of our knowledge as regards the nature of the material basis of living things. Study of polarity from the anatomical point of view has supplied us with basic facts. Advances in other fields, as electrophysiology and biochemistry, especially enzymology, have been considerable, but their critical correlation with the results of past and future experimental morphological research is still forthcoming as an urgent task of botanical investigation. Vöchting regarded protoplasmic constitution as the fundament of cellular and organismic polarity, but at the time little information was available as to its nature in physico-chemical terms. Klebs (108), similarly, spoke of the influence of external and internal factors on the "specific structure", rather emphasizing the dynamic or fluid character of polarity and pattern, and the possibility of modifying them. Morgan (154) saw the problem embodied in the "stereometry" of the bioplasm. The concept that polarity and differentiation are basically static and structural, and related to the molecular and colloidal character of protoplasm or certain parts of it has been frequently emphasized by modern investigators. Frey-Wyssling (63) dealt with the problem from the micellar point of view; other workers emphasized the immense importance of the

cell surface for cellular polarization and depolarization, and the molecular orientation at surfaces and interfaces with reference to either changes in cell shape and movement of cells (*e.g.*, 204), or the structure of the plant cell wall (175*a*, 176, 177). According to Needham (157) and Seifriz (207, 208), the paracrystalline properties of cytoplasm are important for the determination of the character of organized anatomical structures. This state allows for a wide range of morphogenetic possibilities, and the latter author expressed the opinion that polarity of cells and symmetry of organisms must result from it. Harrison's (83, 84, 85) hypothesis of embryonic development and differentiation employs as a basis an activity pattern, genetically controlled but ultimately resulting from the character of chemically polar, symmetrical or asymmetrical protein molecules which produce different substances, subject to electrophoretic transport and localization at opposite poles.

CONCLUSION

The evidence presented in the first part of this paper leads to the conclusion that, granted molecular protoplasmic symmetry relations of the types just indicated exist, their axes must be directable by external factors. Tracing the results of such orientation or reorientation in the individual cytoplasm appears to be possible, at least in a number of representative cases. These include, for example, unicellular and multicellular forms, as zygotes of *Fucus*, spores of *Equisetum*, microspores of seed plants and perhaps the processes in the thalli of *Bryopsis* and *Caulerpa*; furthermore, apical cells of some bryophytes and pteridophytes. Cytoplasmic polarization and reorientation is very conspicuous during wound healing, dedifferentiation and regeneration in large somatic tissue cells, in which it may be assumed that intercellular correlations have become more or less fixed and polarity attained a comparatively static nature. Thus Pfeffer's concept of an unstable state of polarity in cells of apical meristems may well be extended even to older, more highly differentiated cells, for it appears that under conditions of dedifferentiation and regeneration the dynamic, physiological factors which initiate polarity are often capable of obliterating or overcoming comparatively high degrees of wall differentiation and other factors of a static nature, which have induced a rather stable, but not entirely irreversible, state of morphological polarity in the cells.

To determine how polarity manifests itself in the different physiological activities at the cell surface and in the cytoplasm as well as in the submicroscopical and visible morphological properties of plant cells must be the object of further analysis. These properties of the cell can no longer be thought of as a simple axiate relation, such as a shoot end-root end polarity, for each cell possesses or frequently retains the capability to develop the entire plant pattern with its various manifestations of polarity in the individual cells differently directed in relation to each other. While it is possible in a number of cases to direct or redirect through external differentials or initiators the early stages of polarity in unicellular forms or in embryonic development of multicellular plants, it appears much more difficult to change the nature of this relatively well fixed innate pattern of polarities, as expressed in the specific ontogenetic interrelations of the individual cells with regard to plane of cell division, growth, etc. A glance at the remarkable orderly and stable manner of growth in many apical meristems, for example, in *Fontinalis* or *Equisetum*, brings to full realization that factors are at work here, about which at present little is known.

In the multicellular body function and polar character of the individual units appear thus determined by their position or place which they occupy in the general pattern. Instances of polarity first noted and still most familiar to botanists are extreme reactions, such as polar reconstitution of multicellular structures and highly specialized organs; polarity is generally present, however, in much less conspicuous and more gradual form. Its phenomena appear here as expression of the general ones of pattern and differentiation, of which polarity forms only a part or one aspect. Its investigation, therefore, may be expected to provide us with a comparatively simple approach to these difficult biological problems.

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OSMOSIS AND OSMOTIC PRESSURE

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DEFINITIONS OF OSMOSIS

Holman and Robbins (74) have stated that "the word osmosis has been given such a variety of meanings by those who have used it that it has lost any precise meaning whatever" and that "as far as possible, we shall avoid its use". "There exists", Fuller (54) has written, "considerable dispute among scientists as to the exact definition of this term [osmosis]". Livingston (112) has pointed out that "the word osmosis, frequently encountered in connection with the diffusion of substances through membranes, should be dropped, for it does not add to clearness and is frequently confusing". "A definition of osmosis", according to Seifriz (130), "will depend somewhat on one's point of view". Stark (137) has interrogated: "that it (the term, osmosis) has been badly used, or rather misused, is evident, but should it be abandoned for this reason?" "This word", according to Stanford (136), "unfortunately, has been very loosely used and variously defined. In lack of a better term, it will be used in this text for the diffusion phenomena above mentioned".

An analysis of discussions on osmosis in textbooks of botany, plant physiology, animal physiology and chemistry was made. It was found that there are four definitions for osmosis commonly in use (47): (1) osmosis is the diffusion of a solvent (water) through a membrane; (2) osmosis is the diffusion of a liquid or liquids through a membrane; (3) osmosis is diffusion through a membrane; (4) osmosis is diffusion of a substance or substances (solvent and solutes) through a membrane. Two other definitions were also found: (5) osmosis is the process by which osmotic pressure is developed and diffusion of solute molecules hindered; (6) osmosis is diffusion of dissolved substances through membranes. Tabulations of the definitions are given in Tables I and II.

In the second definition, liquid may mean solvent or solution of solvent and solutes. If liquid refers to solvent only, then the second definition is the same as the first. If, however, liquid refers to both solvent and solutes, then the second definition is definitely similar to the third and fourth. It is highly probable that some textbook

authors inferred liquid to be both solvent and solutes. The terminology, hence, is rather vague, ambiguous and confusing. The third definition implies that osmosis is a diffusion of a substance or any substances (solvent and solutes) through a membrane, and so it is quite similar to the fourth, which by several was expressed as the passage of a liquid and its solutes or the diffusion of gases or liquids through a membrane.

If osmosis is said to be diffusion of a liquid through a semipermeable membrane, then it is understood not too plainly that the solvent is the only portion of the solution diffusing through the membrane. By definition, semipermeable means that the membrane thus characterized is permeable to the solvent and not to the solute. In actuality most membranes are slowly permeable to the

TABLE I
DEFINITIONS OF OSMOSIS BY SUBJECTS

Definitions	General botany	Plant physiology	Animal physiology	Chemistry	Total
No. 1	11	5	10	22	48
No. 2	7	2	6	3	18
No. 3	7	1	1	1	10
No. 4	10	5	8	4	27
No. 5	0	0	0	1	1
No. 6	0	0	0	1	1
Total	35	13	25	32	105

solute or solutes. This is another way in which ambiguity arises. It is preferred that the term "differentially permeable" be used to denote the permeable character of membranes variously penetrable to molecules of different substances.

Chemists almost unanimously define osmosis as diffusion of a solvent through a membrane. Inasmuch as almost all chemists and a goodly number of biologists define osmosis as diffusion of a solvent (water) through a membrane, might it be possible for all of us to agree to use this same definition? To be scientific, uniformity in usage of the word should be agreed upon. With osmosis referring to the passage of only solvent molecules through a membrane, the term "dialysis" can be employed very appropriately to refer to passage of solute molecules through membranes.

TABLE II
DEFINITIONS OF OSMOSIS BY AUTHORS

Defi- nitions	Biologists	Chemists
No. 1	Bayliss (1919), Bergen and Davis (1907), Bonar, Holman, and Roush (1938), Brubaker (1913), Burton-Opitz (1920), Cook (1936), Coulter (1910), Coulter, Barnes, and Cowles (1910), Fuller (1941), Greisheimer (1936), Halliburton (1919), Haupt (1932), Hill, Overholts, and Popp (1936), Holman and Robbins (1938), Hylander and Stanley (1941), Loomis and Shull (1939), Macleod (1930), Martin (1917), Meyer and Anderson (1939), Miller (1931, 1938), Seifriz (1938), Seward (1932), Stewart (1914), Transeau, Sampson, and Tiffany (1940), Yokum (1937), Zoethout (1935).	Anderson (1939), Babor and Lehrman (1941), Black and Conant (1924), Briscoe (1937), Cartledge (1929), Cole (1926), Deming (1935), Getman (1931), Getman and Daniels (1937), Gordon and Trout (1940), Gucker and Meldrum (1942), Lincoln and Banks (1928), McCutcheon and Seltz (1929), McPherson, Henderson, Fernelius, and Mack, Jr. (1940), Meldrum and Gucker (1936), Mellor (1922), Reedy (1938), Richardson and Scarlett (1940), Schock and Felsing (1938), Taylor (1927), Tweney and Hughes (1940), Webb (1936).
No. 2	Andrews (1903), Atkinson (1905), Bergen (1901), Brown (1884), Clute (1909), Coleman and Dana (1900), Dearborn (1908), Ganong (1929), Goodale (1885), Hutchison (1881), Kraemer (1914), Stanford (1937), Steele (1889), Thomas (1865), Vines (1886).	Elder (1941), Morley and Muir (1906), Noyes (1913).
No. 3	Brown (1935), Child (1939), Fisk and Addoms (1935), Hall (1905), Payne (1912), Pool (1940), Stark (1928), Yokum (1937).	Hammarsten and Hedin (1914).
No. 4	Colton (1907), Densmore (1920), Dorland (1925), Eyster (1932), Gager (1926), Green (1907), Haupt (1932), Howell (1936), Kerner and Olivet (1895), Kimber and Gray (1925), Martin (1895), Maximov (1930), Palladin and Livingston (1926), Parshley (1940), Peirce (1903), Pool and Evans (1928), Rettger (1916), Sinnott (1935), Smith <i>et al</i> (1936), Tigerstedt and Murlin (1906), Vines (1895), Williams (1925), Youngken (1923).	Brinkley (1933), Fournes (1873), Hackh (1937), Kendall (1937).
No. 5		Chapin and Steiner (1938).
No. 6		Tottingham (1935).

OSMOTIC PRESSURE CONCEPTS

"Osmotic pressure" has had and still has a variety of meanings, all of which breed ambiguity and misunderstanding.

The phenomenon was first observed by Abbé Nollet in 1748 and then by Dutrochet in 1827. Dutrochet described the escape of zoospores from an alga. In trying to arrive at an explanation for the bursting of the sporangium, he supposed that increased absorption of water by the sporangium was brought about by water-attracting substances within, and that this caused the rupture. If a pollen grain filled with sugar solution and colloidal particles of proteins is placed in water, the solvent enters, and the outwardly directed hydrostatic pressure simultaneously developed may become so great as to rupture the pollen grain. Rupture of the algal sporangium, as observed by Dutrochet, was caused in a similar way. In short, Dutrochet regarded osmotic pressure to be hydrostatic or turgor pressure.

Pfeffer (1877) performed the classical researches on osmotic pressure. He used precipitated copper ferrocyanide membranes in or on the walls of a porous pot to which a glass rod was attached vertically and in which a 10% solution of cane sugar was placed. The pot was then placed in water which at once began to enter through the wall, and the diluted sugar solution began to rise in the tube. A U-tube was filled with mercury and connected with the pot which had been coated with a copper ferrocyanide membrane. It showed that the water entered with a force sufficient to raise and support a column of mercury of considerable height. Pfeffer considered the water pressure supporting the column of mercury to be osmotic pressure, and explained it by postulating an attraction between the molecules of sugar in the porous pot and the molecules of water outside.

Van't Hoff (151) studied the results of Pfeffer carefully. He concluded that the dissolved substances were giving pressures in the same way that a gas exerts pressure, and that osmosis was a molecular phenomenon comparable to the pressure exerted by gases when confined. At standard conditions of temperature and pressure (0° C. and 760 mm. of pressure), a gram molecular weight of cane sugar dissolved in 22.4 liters of water at 0° C. should give an osmotic pressure of one atmosphere, and if confined to one liter of water, should correspondingly give 22.4 atmospheres of pressure.

Van't Hoff found these conditions to exist. Since then it has been the opinion of many that osmotic pressure is caused directly by impact of the molecules of the solute upon the membrane. McCutcheon and Seltz (95), chemists, clearly depict this idea by stating that "when a solution is separated from some of the pure solvent by a semi-permeable membrane, which permits the free passage of the solvent but not the solute, the molecules of the solute, by impact upon this membrane, exert a pressure similar to the pressure of the molecules of a gas upon the walls of the vessel" and that "the pressure produced in this manner is called the osmotic pressure of the solution".

Including this archaic and thermodynamically unsound idea of osmotic pressure, there are eight different concepts of the term: (1) osmotic pressure is the diffusion pressure of the solute molecules; (2) osmotic pressure is hydrostatic pressure or turgor pressure; (3) osmotic pressure is the actual maximum hydrostatic pressure developed; (4) osmotic pressure is the capacity of a substance to produce a given maximum hydrostatic pressure, just as one speaks of the horsepower of an engine to indicate the potential power of the engine; (5) osmotic pressure is theoretical mechanical pressure exactly equal and opposite to the tendency of pure solvent to diffuse into a solution of same solvent; (6) osmotic pressure is the pull that the cell sap is capable of exerting upon pure water if it were separated from it by a perfectly semipermeable membrane; (7) osmotic pressure is the diffusion pressure of solvent (water) molecules passing through a membrane, or the pressure responsible for the movement of solvent; and (8) osmotic pressure is the difference in diffusion pressure of the solvent on both sides of the membrane (94), or, as Holmes (75) stated it, "osmotic pressure is the pressure required to stop the movement of solvent through a semi-permeable membrane from a more dilute to a more concentrated solution." The eight definitions of osmotic pressure are statistically presented in Tables III and IV.

"Net osmotic pressure" or "effective osmotic pressure" (133), "suction force" (150), "suction pressure" (140), "suction tension" (8), "turgor deficit" (38), "diffusion pressure deficit" (104), and "water absorptive power" (143) are terms which have been used to describe the osmotic properties of solutions in cells. Most of these terms fit appropriately into definitions No. 6 and No. 8.

"Turgor deficit" and "diffusion pressure deficit" are not the same as osmotic pressure, except under limited conditions. "Diffusion pressure deficit" is equal to osmotic pressure only when "all parts of the system are under the same temperature and under the same external (turgor and atmospheric) pressure" (105). Disregarding slight differential shades of meaning, all of these aforementioned terms are broadly synonymous and have very much the same meaning as "diffusion pressure deficit". The fact that some of the terms fit into a few of the enumerated definitions of osmotic pressure and others do not, is due to the connotation, explanations, and somewhat diverse concepts of each term, and to the functional mechanism implied by each definition.

The earliest definitions or versions of the term (osmotic pressure) are that it is the hydrostatic pressure or turgor pressure, and that it is the diffusion pressure of the solute molecules of the solution. Plant physiologists of today favor the fifth definition more

TABLE III
DEFINITIONS OF OSMOTIC PRESSURE BY SUBJECTS

Definitions	General botany	Plant physiology	Animal physiology	Chemistry	Total
No. 1	0	1	3	15	19
No. 2	2	5	1	5	13
No. 3	1	0	9	8	18
No. 4	0	6	3	2	11
No. 5	0	7	1	21	29
No. 6	0	3	1	0	4
No. 7	5	2	5	2	14
No. 8	0	1	0	1	2
Total	8	25	23	54	110

than any other. This definition states that osmotic pressure is theoretical mechanical pressure exactly equal and opposite to the tendency of solvent to diffuse into a solution of same solvent. Chemists strongly adhere to definitions one and five with a statistical preference for number five. A comparatively large proportion of general botanists favor the seventh definition which states that osmotic pressure is the diffusion pressure of solvent molecules passing through a membrane. Functionally, this is the fundamental basis of osmotic pressure and is the cause of the resulting hydrostatic or turgor pressure. Lyon (94) and Holmes (75) are about

the only individuals who have put the eighth definition in writing. It is interesting to note that, while most botanists and chemists maintain that osmotic pressure is affected only by solute concentration, Dr. Lyon goes a step further and contends that hydrostatic pressure also exerts an influence. In 1938 the author had an interesting series of correspondence with Dr. Lyon in regard to definitions and concepts of osmotic pressure, and has been successful in pointing out that osmotic pressure is a resultant of both hydrostatic pressure and solute concentration and not merely the resultant of solute concentration, but failed in another respect. Dr. Lyon refused to go the whole way in making osmotic pressure synonymous with the diffusion pressure of the solvent.

Since it is difficult to change a definition of a term, it is recommended that we use the term "osmotic diffusion pressure", and define it as the diffusion pressure of a solvent diffusing through a membrane. Although it is difficult to measure the exact magnitude of the force and to express it in atmospheres of pressure, it may be expressed in molarity of a cane sugar solution. For example, if the diffusion pressure of the water in a given solution is equivalent to the diffusion pressure of the water in a .35 M cane sugar solution, then the osmotic diffusion pressure of the water in the solution might be said to be .35 M. The term "osmotic pressure" could still be used to designate a potential maximum hydrostatic pressure. The author is very much concerned that the term be retained with this meaning.

The term "osmotic diffusion pressure" would make it unnecessary to use the terms "suction force", "suction tension" and "diffusion pressure deficit" which have never been popular and fully desirable (94) and which are unwieldy (91). Knowing the osmotic diffusion pressure of the water in each of two solutions separated by a membrane, it is simple to determine the direction of the general flow of water. While water diffuses in both directions through a membrane which separates solutions of different concentrations, more water always diffuses from the solution with the greater osmotic diffusion pressure to the solution with the lesser osmotic diffusion pressure. External pressures being equal, distilled water has the greatest osmotic diffusion pressure. Osmotic diffusion pressure is affected by temperature, pressure such as hydrostatic pressure or turgor pressure, and solute concentration.

TABLE IV
DEFINITIONS OF OSMOTIC PRESSURE BY AUTHORS

Definitions	Botanists	Plant physiologists	Animal physiologists	Chemists
No. 1		Livingston (1903).	Brubaker (1913), Hill (1908), Loeb (1906).	Beutner (1933), Cameron (1928), Cameron and Gilmour (1935), Chapin and Steiner (1938), Fearon (1940), Hackh (1937), Hammarsten and Hedin (1914), Jones (1907), McCutcheon and Seltz (1929), Millard (1936), Nernst (1923), Prescott and Johnson (1901), Steel (1928), Tweney and Hughes (1940), Van't Hoff (1887).
No. 2	Densmore (1920); Strasburger <i>et al</i> (1912).	Coulter, Barnes, and Cowles (Shull, 1930)*, Dutrochet (1827), Jost (1907), Maximov (1930), Palladin and Livingston (1926).	Bayliss (1919).	Findlay (1933), Getman (1931), Lincoln and Banks (1928), Mellor (1922), Tottigham (1935).
No. 3	Hill, Overholts and Popp (1936).		Burton-Opitz (1920), Evans (1930), Hall (1905), Macleod (1930), Pearce and Macleod (1924), Porter (1906), Stewart (1914), Tigerstedt and Murlin (1906), Zoethout (1935).	Alexander (1937), Cole (1926), Deming (1935), Gordon and Trout (1940), Kendall (1937), Reedy (1938), Shaw (1941),* Webb (1936).
No. 4		Coulter, Barnes, and Cowles (1910), Meyer (1938), Meyer and Anderson (1939), Miller (1931), Raber (1930, 1936), Seifriz (1938)*.	Halliburton (1919), Hickman (1930), Ponder (1929).	Bodansky (1938), Gucker and Mel-drum (1942)*.

* Some authors present two or more definitions.

TABLE IV.—(Continued)

Def- initions	Botanists	Plant physiologists	Animal physiologists	Chemists
No. 5		Barton-Wright (1933), Beck (1928), Blackman (1921), Findlay (1913), Loomis and Shull (1939), Miller (1938), Seifriz (1938).*	Hawk and Bergeim (1937).	Anderson (1939), Babor and Lehrman (1941), Brinkley (1933), Briscoe (1937), Cartledge (1929), Callender (1908), Creighton (1935), Curtman (1931), Elder (1941), Gucker and Meldrum (1942),* Lewis (1921), Lewis and Randall (1923), Lowry (1907), Mathews (1931), McPherson, Henderson, Fernelius, and Mack, Jr. (1940), Porter (1917-18), Noyes (1913), Schock and Felsing (1938), Shaw (1941),* Taylor (1927), Thompson (1939).
No. 6		Ganong (1929), Miller (1931),* Pfeffer (1877).	Best and Taylor (1937).	
No. 7	Brown (1935), Holman and Robbins (1938), Payne Stanford (1937), Yokum (1937).	Coulter, Barnes, and Cowles (Shull, 1930),* Eyster (1940).	Dorland (1925), Hemmeter (1912), Howell (1936), Martin (1917), Williams (1925).	Meldrum and Gucker (1936), Richardson and Scarlett (1940).
No. 8		Lyon (1941).		Holmes (1941).

* Some authors present two or more definitions.

Increase in temperature magnifies the osmotic diffusion pressure, and increase in hydrostatic pressure or turgor pressure increases the osmotic diffusion pressure, but increase in solute concentration diminishes the osmotic diffusion pressure. Temperature is usually an insignificant factor in affecting the osmotic diffusion pressure of water in cell sap of plant cells. Due to added external pressure or turgor pressure, a .1 M solution may contain water with a greater osmotic diffusion pressure than a 0 M solution (distilled water). In this case the major trend of water diffusion, if separated by a differentially permeable membrane, would be from the former to the latter. External pressures or turgor pressures being equal, the distilled water would have the greater osmotic diffusion pressure, and the major trend of water diffusion would be from the distilled water into the .1 M solution.

The term "activity" (92) can be used in place of osmotic diffusion pressure. In this case, the major trend of osmotic water diffusion would be from the side of the membrane where the water molecules are more active to the side where the water molecules are less active.

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Vegetational Zonation in the Rocky Mountains ...	R. F. DAUBENMIRE <i>University of Idaho</i>
Geographical Distribution of Fungi	G. R. BISBY <i>Imperial Mycological Institute, Kew</i>
Plant Life and the Law of Man. IV. Barberry, Currant and Gooseberry, and Cedar Control ...	E. H. FULLING <i>The Botanical Review</i>
The Cuticle in Angiosperms	J. H. PRIESTLEY <i>University of Leeds</i>
Lichens—Their Biological and Economic Significance	G. A. PEREZ-LLANO <i>Harvard University</i>
Root-rots of Some Non-cereal Crops	G. H. BERKELEY <i>Dominion Laboratory of Plant Pathology</i>
Recent Developments in the Classification of Bacterial Plant Pathogens	CHARLOTTE ELLIOTT <i>Bureau of Plant Industry</i>

Articles arranged for most recently

Cytogenetics of Nicotiana	T. H. GOODSPEED <i>University of California</i>
Tundra Vegetation	R. F. GRIGGS
Cytology and Genetics in Relation to Taxonomy ..	C. L. HUSKINS <i>University of Toronto</i>

Articles in course of preparation

The Cytology of Fertilization in Angiosperms ...	L. E. ANDERSON <i>Duke University</i>
Development of the Madre-Tertiary Flora	D. I. AXELROD <i>University of California</i>
Relation of Wood Anatomy to Taxonomy	I. W. BAILEY <i>Harvard University</i>
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